

a brief notice ; it is this : “ Spiders are reputed to be subject to the *stone* : I do not say *Calculus in Vesica* ; but we are informed by Lesser that Dr. John Franck having shut up fourteen spiders in a glass with some valerian root, one of them voided an ash-coloured calculus with small black dots.” This singular opinion seems to have originated in a misapprehension of an ordinary occurrence, which I shall proceed to explain. If the *fæces* of spiders, which consist of a white fluid comprising black particles of greater density, happen when voided to be suspended in the webs or among the lines spun by these animals, they assume, under the influence of molecular attraction, the spherical figure common to fluids in general when similarly circumstanced, and soon becoming indurated by desiccation, a change of colour from white to gray or grayish brown spotted with black uniformly takes place, and in this state they constitute, I doubt not, the substance which Dr. Franck mistook for a calculus.

XVIII.—*On some Points in the Structure and Growth of Monocotyledons.* By ARTHUR HENFREY, F.L.S. &c.*

[With two Plates.]

ALTHOUGH the views which are advocated in the following paper do not possess much originality, I have been induced to lay my observations before this Section by several considerations. In the first place, I believe that the subject is one to which a comparatively small amount of attention has been paid in this country, and therefore, dependent as we have been on foreign observers for our knowledge of it, indigenous investigations may have some interest ; secondly, the theories of monocotyledonous structure held by the chief continental authorities are at present not generally-received views, but to some extent individual opinions, conflicting more or less one with another ; and, lastly, as I have devoted a considerable amount of time to the examination of this most intricate subject, I have thought that independent observations, carefully and repeatedly made, might by their publication be of some service to the science of Botany, either by pointing out the errors or confirming the statements of other anatomists.

I have directed my attention to the structure of those Monocotyledons which can be readily obtained in a living state in this country ; the structure of the stems of Palms I have not had the opportunity of studying, and therefore with regard to them I have been obliged to depend upon the observations of others. So

* Read at the Meeting of the British Association, June 1847, and communicated by the Author.

far as I can at present judge, the various forms are all reducible to two types, which are themselves united under the single common character which was first definitely announced by Schleiden.

Those who are acquainted with his views will recollect that he has pointed out an essential distinction between the characters of the fibro-vascular bundles of Monocotyledons and of Dicotyledons, which in the former are *closed*; that is, their growth in the transverse direction is arrested at a definite epoch, whence results their isolated condition, giving a peculiar aspect to the monocotyledonous stem; while in the Dicotyledons the fibro-vascular bundles not only grow laterally, so as to come in contact with one another as wedge-shaped bodies collectively forming a ring, but their peripheral or external face is capable of development to an extent only limited by the life of the plant in which they exist. Thus the successive layers which add to the thickness of a dicotyledonous stem are produced by the peripheral growth of the fibro-vascular bundles, the distinction into rings, frequently so strongly marked, depending merely on the difference of the condition of those elements of the fibro-vascular bundle produced in the earlier part of the year from that of those formed during the advance of the season.

This is the sole universal character by which the stems of the two great classes can be distinguished. The theoretical distinction into Endogens and Exogens has not a single fact to support it. All plants possessing a stem are Endogens so far as the origination of organs is concerned, since these are developed in buds in the axils of older organs, and, in terminal buds, are immediate developments of the central parenchyma. But the new deposits of fibro-vascular structure belonging to these are found crossing those of the older organs at the earliest period of their development, and always and in all stems come to be applied upon their outer surface. The accounts of endogenous growth are negatived by all those who have traced the development of structure in the Monocotyledons, and could only have been founded on a superficial examination of fully-formed stems. I have traced the development in the buds of many of our indigenous and commonly cultivated Monocotyledons, and they all agree with the characters of that one which I have selected to illustrate this point.

In the accompanying drawings (Pl. IX. figs. 2 and 3) are represented sections of very young buds of *Sparganium ramosum*, and the nascent fibro-vascular bundles are seen in the central portion; the uppermost and youngest, much more delicate and less perfect than the lower, being in direct connexion with the central nascent leaves. The figures also illustrate several other important points concerning the structure of monocotyledonous

stems, of which I shall have presently to speak ; before passing to these, however, I must refer to the controversies which exist as to the course of development, in time, of the different portions of the fibro-vascular bundles. Von Mohl offers, I believe, no opinion on this point ; Schleiden states that their development commences below and extends upwards into the leaf, in which opinion he is borne out by the statements of several authors, particularly Mirbel* and Naudin†. Gaudichaud‡ states that the development begins in the centre, and that an ascending and a descending portion are gradually organized, one passing to the leaf, the other to the roots.

My own observations are in favour of the former opinion, and indeed Gaudichaud's publications are wanting in proper scientific completeness. His statements are much too dogmatic, and his figures have too much of the character of diagrams, to be received as direct evidence in a case where such complex structures are in question.

In the very youngest part of the bud the nascent leaf is wholly cellular ; the cells have generally a spherical form, like those of the other organs and of the conical summit of the stem ; the whole are clothed by a delicate epithelium. But in the substance of the stem and nascent leaves are to be remarked certain regions, where the cells, in the earliest condition I have seen them, have a peculiar appearance, being elongated and arranged in parallel rows (Pl. X. fig. 1 *a, a*) ; in the centre of these bundles of elongated cells first appear the vessels, which are at first unrollable spiral vessels ; these regions are in fact the nascent fibro-vascular bundles. These fibro-vascular bundles appeared to me to be always younger and less perfect as they approached the apex, or *punctum vegetationis*. The further development of these elements into the ducts and woody structures found in full-grown bundles I have not systematically followed, as I was more particularly anxious to attain a clear view of their anatomical relation to each other and to the roots.

The condition of the relations of the bundles above indicated is the same as that which exists in most bulbs, and is the form which gives the type characterized by Schleiden as consisting of a stem where the internodial portions are little or not at all developed. I believe that the stem of a solid Palm has essentially the same relative arrangement of the parts. The other type is found in some Palms and in the annual stems of Grasses ; this is characterized by the development of the internodes.

In regard to the flowering-stem of the first form we have two modifications to discriminate, depending on the position of the

* Ann. des Sc. Nat. 2 sér. xx. 6.

† Ibid. 3 sér. i. 162.

‡ Recherches gén. sur l'Organographie, &c. Paris, 1841.

points where the leaves pass off from the stem, in the full-grown annual stem. In the *Crocus*, *Tulip*, *Hyacinth*, &c., the leaves arise immediately from the base of the flattened stem situated at the bottom of the bulb; the fibres of the peduncle of these plants become developed upwards with the growth of the part in which they are placed, their inferior extremities retaining their relations unaltered below. In the *Tiger Lily*, *Crown Imperial*, &c., the leaves are borne upon the elongated stem, and in *Asparagus* branching of the stem takes place; in this form the lower part of the stem retains the bulb-like character, and the ascending portions of the fibro-vascular bundles become developed upward in the stem before passing into the leaves.

Such stems, examined without reference to the bulb and in the full-grown state, would be liable to be taken for instances of an endogenous growth, since the fibres of the lowest leaves or branches are most external, and those going to the younger leaves and flowers, situated in the centre; but by tracing them downward to the base in the bulb, we there find them crossing to get outside the older fibres. Some of the fibres in the upper part of the stem appear to possess no inferior tract; these may be supposed to originate subsequently during the growth of the flowering-stem, and do not interfere with the general character of the structure.

In speaking of crossing, it must always be recollected that this term is used rather loosely, as the upper bundles take very variable courses to get to the outer side of the lower ones; sometimes their lower tract is found on the side opposite to that on which they ascend, and they succeed one another spirally, so that it is only here and there that a section will exhibit a direct crossing like that usually shown in diagrams.

In the above-mentioned plants the annual stem may be regarded as an inflorescence. In the Grasses and in *Tradescantia* we find several internodes in the annual stem; the fibro-vascular bundles interlace at the nodes, at these points also new fibres arise, and roots are often given off. These nodes may be compared to bulbs succeeding one another upwards at intervals in the stem. In the creeping rhizomata of many Monocotyledons we have examples of bulbs thus succeeding one another; only in such cases they are axillary and not terminal, and they are the *buds* provided for the next year's growth, retained in connexion with the old stem instead of being shed like the *cloves* of true bulbs. In most instances they are sessile one upon another; but in *Sparganium ramosum* we have an example of bulbs succeeding one another with internodes developed, and thus we get, in a perennial monocotyledonous stem, an analogue of the annual stem of a Grass or of *Tradescantia*; for the principal difference

between the two latter is the fistular condition of the stem in the Grass*.

I next directed my attention to the lower extremities of the fibro-vascular bundles, endeavouring to discover their relations with the fibro-vascular system of the roots. Here we meet with several modifications of arrangement.

In the stems I have examined the lower ends of the fibres appear to branch and to anastomose with their fellows, sometimes forming a distinct fibrous layer. In order to explain the relations of these extremities, I must point out some peculiarities in the cellular system.

Von Mohl has described in the stems of Palms a central region, a fibrous layer, and a cortical region. The analogues of these appear to me to be present in most monocotyledonous stems. The tissue of the central region is generally composed of spherical cells which contain abundance of starch at certain periods; this region, in which lie the fibro-vascular bundles, undoubtedly represents the pith and medullary rays of Dicotyledons. The cells of the cortical region are usually very irregular in form, and have large intercellular spaces; they contain little or no starch.

In bulbs the central region is inclosed by rather a thin layer of the cortical parenchyma, which is continuous with the bases of the coats or scales; the line of junction of the two regions is indicated in the very youngest state of the bulb by a darker colour and greater density of the tissue. At this line the fibro-vascular bundles terminate below, and their extremities, by branching and anastomosing, frequently produce a dense layer, the "fibrous layer" of Von Mohl. The cortical region cannot be made out in the culms of the Grasses, and it is not continued distinctly into the flowering-stems of bulbs. In *Sparganium ramosum* it is very much developed, both in the nodes and internodes; in the former it exhibits fibres crossing transversely, and thus *weaving*, as it were, the whole into a dense fibrous coat separating the central from the cortical region.

The most important point relating to the fibrous layer is, that it gives origin to the roots, for there is no direct communication between the fibro-vascular bundles of the stems and those of the roots. The bundle which lies in the midst of the root of *Sparganium*, and indeed of all the annual roots I have examined, is composed of a number of vessels arising in a circle from the

* An illustration of this analogy between the nodes of the stem of a Grass and bulbs, physiologically denoting a certain degree of independence, seems to me to be offered by the possibility of *grafting* grasses upon one another at the nodes. This has been effected by an Italian botanist, Caldeirini, in the Millet, and he also successfully grafted Rice upon *Panicum Crus-galli*.—See Ann. des Sc. Nat. Sept. 1816.

fibrous layer; they gradually approach one another as they pass out, thus forming a kind of funnel-shaped body. The central parenchyma is gradually converted into ligneous cells as the tube of vessels extends outwards (Pl. X. figs. 2 and 3), and the root at a short distance from its point of origin presents in a cross section a central cylinder of wood having a ring of vessels near its periphery, the whole being inclosed in a parenchyma continuous, near the fibrous layer, with the cortical layer of the stem. When the roots produce branches the latter are given off at right angles (Pl. X. fig. 2), and arise on the central fibro-vascular cylinder, bursting their way through the cortical parenchyma of the root as the main roots do through the outer part of the cortical layer of the stem. When the roots fall off, they leave orifices in the stem where they have thus burst through. Roots appear very early in the buds, in fact contemporaneously with the leaves. In the section of the apex of a bud of *Sparganium* (Pl. IX. fig. 3) they are seen in the nascent condition. It is disputed whether the fibro-vascular bundles are first perfected where they are in contact with the fibrous layer, or whether their bundles are formed independently and afterwards effect a junction. With regard to the roots of *Sparganium*, just noticed, I believe their central bundle is organized contemporaneously and in continuity with the fibrous layer.

The fibrous layer is not so distinctly marked in bulbs like the Tulip and Hyacinth, or in tuberous-rooted Monocotyledons like Asparagus and the terrestrial Orchidaceæ. The ends of the fibro-vascular bundles of the stem are found branching and anastomosing at the line of junction of the cortical and central regions, and the bundles of the roots are in connexion with these plexuses. The tubers of *Orchis mascula* are merely enlarged roots; the difference between them and the other roots arises from the development of the central (otherwise ligneous) portion into a parenchymatous mass, which breaks up the ring of vessels, and carries them to the outer region of the tuber.

The development of successive roots taking place from below upwards, the younger roots arise from parts of the fibrous layer in relation with the younger fibro-vascular bundles. In cases where the internodes are developed, roots and buds are commonly produced at the nodes, as in *Tradescantia*, Grasses, and *Sparganium*; in the latter, roots are also formed irregularly on the internodal parts of the stem* (Pl. IX. fig. 1 shows the scars left by their fall).

* The *endorhizal* mode of producing roots seems to be a constant character of Monocotyledons as well in the full-grown condition as in the embryo. It is also found in Nymphæaceæ, which present many points of affinity with monocotyledonous structure.

There is another point in the structure of Monocotyledons which does not appear to me to be clearly understood. In the cortical region are often found fibrous bundles, passing into the leaves above, and which, in the cases I have examined, possess no vessels, and consequently have the character of liber bundles. In *Sparganium ramosum* they are very numerous and of considerable size; they are also found in the Grasses, and apparently in all such stems as have the internodial portions developed. I cannot find them in bulbs, or in such rhizomes as the common Iris; but in the flowering-stem of many such plants, *ex. gr.* the Tulips, Crown Imperial, Tiger Lily, &c., the parenchyma gradually changes its character towards the periphery, and just within the epidermal layers it consists of long fibrous cells exactly resembling liber cells. This ring of woody cells is very much developed in *Tamus communis* and *Smilax aspera* (and I believe in most plants belonging to the same orders), and has been taken for a layer of wood analogous to that of Dicotyledons; but this is certainly a misconception, as it is distinctly defined at its outer border, and does not present the slightest trace of a developing or cambium layer. Internally it passes insensibly into the central parenchyma of the stem, in which lie the true woody bundles having vessels as usual. If this has an analogue at all in Dicotyledons, it is the liber; and there are many reasons in favour of such an hypothesis, especially if we consider it as identical with the fibres of the cortical layer of such stems as *Sparganium*.

In conclusion, adverting to the discussions as to the mode of increase of the stem of Monocotyledons, it seems to me that many writers do not sufficiently consider the peculiar characters of this organ. This question must not at all be mixed up with that of the formation of new layers of wood in Dicotyledons, since in all the usual forms (making exception of such as *Dracæna*, *Cordyline*, &c.) nothing analogous to the second year's layer of wood is ever produced. In bulbs the buds are thrown off; in branching rhizomes they become independent physiologically, and the old stem never increases; while in the Palms, the bud, though continually developing, merely applies a new layer spirally upon the pre-existing portions, so that the new growth might be roughly exemplified by a series of hollow cones of *equal* size placed one upon another. Here all growth is analogous to the upward growth of the terminal bud of a dicotyledon; there is no cambium layer, and no peripheral increase*. The

* For every year's development of the terminal bud of a dicotyledon we find a new layer deposited all over the old wood by the cambium layer, forming a new annual ring; in Palms we have merely the terminal shoot without any analogue of the annual ring.

greater consistence which the older parts of the stems of Palms acquire is to be regarded as arising from causes similar to those producing the peculiar characters of the heart-wood of Dicotyledons.

DESCRIPTION OF THE PLATES.

PLATE IX.

- Fig. 1.* A branching rhizome of *Sparganium ramosum*, exhibiting the nodes, *a*, and the internodes, *b*; in the latter the fibro-vascular bundles take straight and parallel courses.
- Fig. 2.* Half of a vertical section through a terminal bud, showing the relative positions of the developing bundles. *a*, the central parenchymatous region, in which the bundles lie; *b*, the line where the fibrous layer is formed by the lower extremities of the bundles; *c*, the cortical region in which lie the liber (?) bundles; *d*, the *punctum vegetationis*.
- Fig. 3.* A similar section; the references are the same; *ee* are nascent roots (figs. 2 and 3 are magnified six diameters).
- Fig. 4.* A portion of the cortical region with liber (?) fibres continued into the leaves.
- Fig. 5.* Vertical section of a full-grown node (like *a* of fig. 1), prepared by maceration, so as to exhibit the fibro-vascular bundles *in situ*. *a*, the bundles; *b*, axillary branches forming the internodal portions (like *b* in fig. 1); *c*, the cortical region, now a mass of fibres; *d*, the fibrous layer, which presents several layers of densely interwoven fibres derived from the lower extremities of the bundles of the central region.
- Fig. 6.* Transverse section of an internode (*b* in fig. 1). *a*, the central region; *b*, the fibrous layer; *c*, the cortical region, here very much developed.
- Fig. 7.* Vertical section of the same. *a*, *b*, *c*, same references; *d*, a root, the central fibro-vascular bundle of which is seen arising from the fibrous layer. The root breaks down the substance of the cortical region when making its way out. The fibro-vascular bundles of the stem are parallel here, and the slender liber (?) bundles are shown in the cortical region *c*.

PLATE X.

- Fig. 1.* Highly magnified vertical section of a bud. *a*, the nascent fibro-vascular bundles.
- Fig. 2.* Transverse section of a portion of an internode. *a*, the central region; *c*, the fibrous layer giving off the vessels to the root *g*; *d*, the cortical region; *e*, liber (?) bundles; *f*, epidermis (enlarged about five times).
- Fig. 3.* Part of the same highly magnified. *a*, the parénchyma of the central region of the stem gradually becoming converted into ligneous cells as it passes into the centre, *b*, of the fibro-vascular bundle of the root; *c*, the ducts which are given off from the fibrous layer to form the vessels of the root; *d*, the cortical parénchyma of the stem.
- Fig. 4.* Magnified section of the cortical region, showing the large intercellular spaces (the cells of this tissue are extremely irregular in form, and contain no starch granules). *e*, a liber (?) bundle.